

# Pursuit and Cohesion: in Nature and by Design

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**ABSTRACT:** Pursuit phenomena in nature have a vital role in survival of species. In addition to prey-capture and mating behavior, pursuit phenomena appear to underlie territorial battles in certain species of insects. In this talk we discuss the geometric patterns in certain pursuit and prey capture phenomena in nature, and suggest sensorimotor feedback laws that explain such patterns. Our interest in this problem first arose from the study of a *motion camouflage* (stealth) hypothesis due to Srinivasan and his collaborators, and an investigation of insect capture behavior in the FM bat *Eptesicus fuscus*, initiated by Cynthia Moss. Models of interacting particles, developed in collaboration with Eric Justh, prove effective in formulating and deriving biologically plausible steering laws that lead to observed patterns.

The echolocating bat *E. fuscus* perceives the world around it in the dark, primarily through the information it gathers rapidly and dependably by probing the environment through controlled streams of pulses of frequency modulated ultrasound. The returning echoes from scatterers such as obstacles (cave walls, trees), predators (barn owls) and prey (insects), are captured and transduced into neuronal spike trains by the highly sensitive auditory system of the bat, and processed in the sensorimotor pathways of the brain to steer the bat's flight in purposeful behavior. In joint work with Kaushik Ghose, Timothy Horiuchi, Eric Justh, Cynthia Moss, and Viswanadha Reddy, we have begun to understand the control systems guiding the flight. The effectiveness of the bat in coping with, attenuation and noise, uncertainty of the environment, and sensorimotor delay, makes it a most interesting model system for engineers concerned with goal-directed and resource-constrained information processing in robotics. The bat's neural realizations of auditory-motor feedback loops may serve as models for implementations of algorithms in robot designs.

While the primary focus of this talk is on pursuit, the results suggest ways to synthesize interaction laws that yield cohesion in collections of particles, treating pursuit as a building block in mechanisms for flocking in nature and in engineered systems.

## Our Subject

Understanding mechanisms (feedback laws, interaction laws) needed to create natural and artificial swarms is of great current interest.

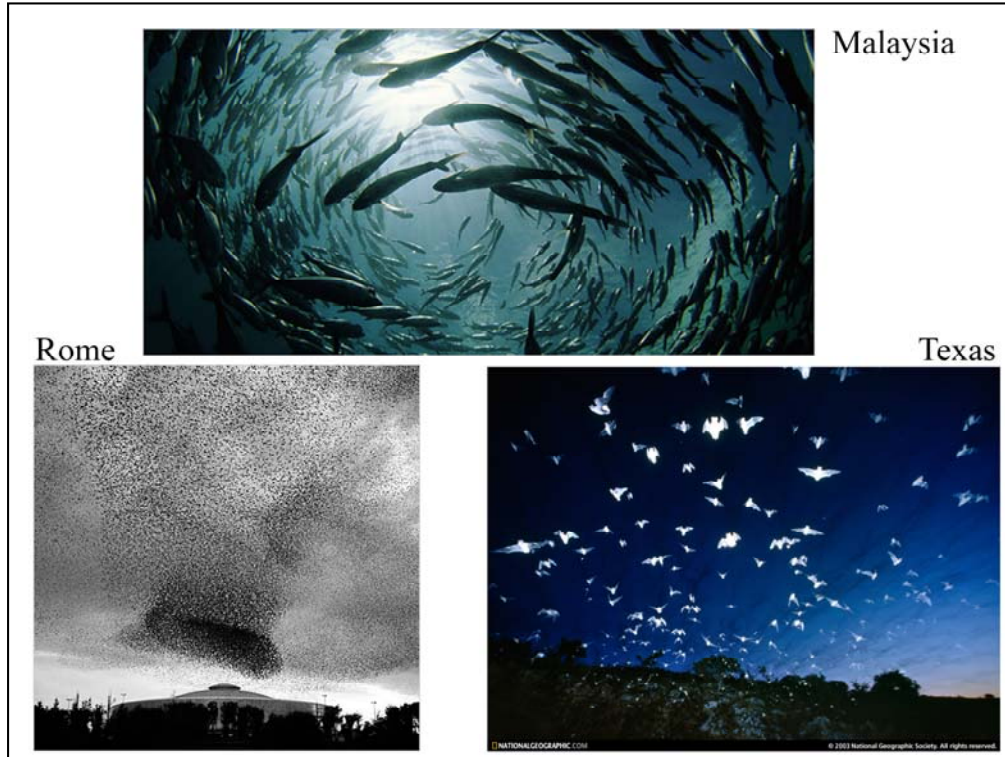
Questions of scalability of such **cohesion laws** have led us to consider non-cooperative interactions.

Pursuit phenomena in nature (e.g. prey capture behavior, chasing possible mates, territorial battles etc.) have a vital role in the survival of species. **Pursuit laws** are feedback laws that realize such non-cooperative interactions.

In collaborative work with biologists, we have explored pursuit phenomena in (a) dragonflies (b) echolocating bats, as problems of **control theory**.

The rich collection of flight data examined in this study has also stimulated solutions to some interesting **inverse problems**.

A theory of swarming (flocking, schooling) is being developed through the work of biologists, engineers, mathematicians and physicists. One of the challenges arising in this work is to properly scale the models involved, as the number of units in a swarm (flock, school) increases. This is not only a problem of mathematical modeling. It is also a problem of biological and technological plausibility. How many locusts (birds, fish) can a member of a swarm (flock, school) pay attention to? Recent work of a European collaboration studying a flock of starlings suggests that small numbers of attentional targets are involved. Once a target is noted, it is hypothesized that a unit approaches the target in a manner akin to pursuit. **Pursuit is a building block** of swarming behavior. Understanding pursuit is our goal.



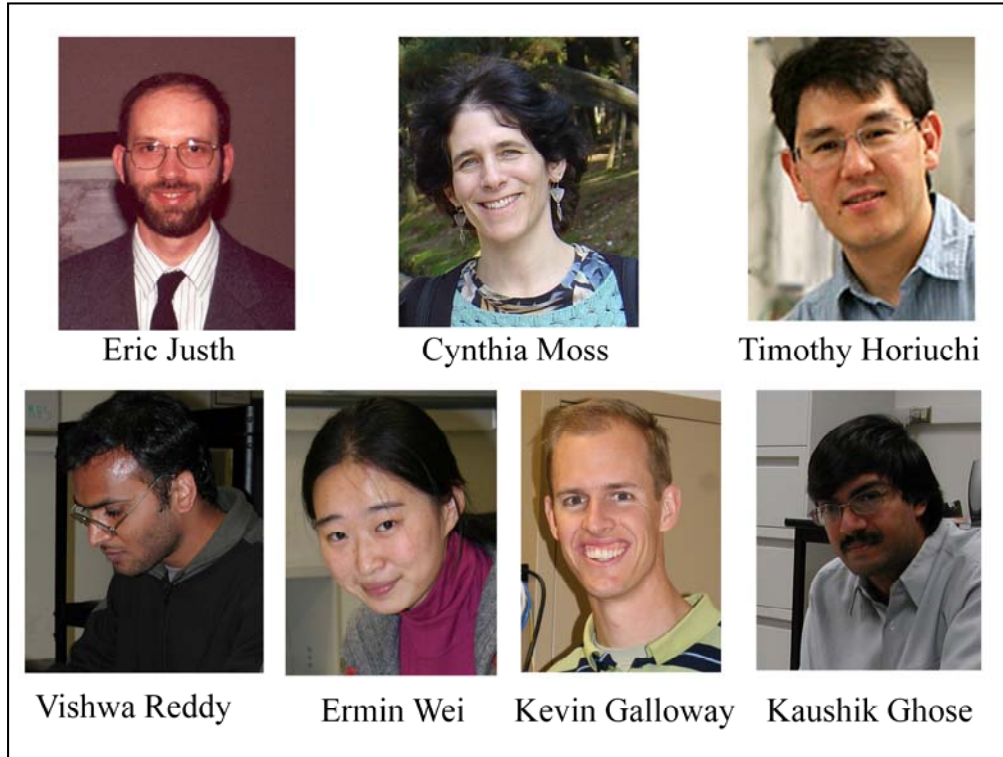
These are pictures from the web. The fish are big eye trevally making a torus school off the coast of Malaysia. The starlings on lower left are over Termini station in Rome, executing amazing changes of shape. The infra red photograph on lower right captures emergence of Mexican free tailed bats from Bracken cave in Texas, on their way to insect feeding high up.

## Bracken emergence



<http://www.batcon.org/home/index.asp?idPage=56>

Click on "[View a short video clip of the Bracken emergence](#)"



My collaboration with Eric Justh on pursuit was built on our earlier work in uncovering cohesion laws. We turned our attention to an interesting hypothesis, known as motion camouflage (due to Srinivasan and Davey, and later Srinivasan, Mizutani and Chahl), about insect flight behavior during aerial territorial battles. We derived control laws applicable to this setting. Separately, I had initiated a collaboration with Cynthia Moss, Kaushik Ghose and Timothy Horiuchi, to understand the flight behavior of echolocating bats during insect pursuit and capture behavior in the laboratory. Remarkably there were geometric properties of bat trajectories that were indistinguishable from those of motion camouflage trajectories. This led to the search for appropriate feedback control laws that guide bat flight. With Vishwa Reddy, we found delayed feedback laws. With Kevin Galloway, we explored the role of stochasticity. More recently, with Ermin Wei, we have found a basis for the observed prevalence of a particular strategy in the case of the echolocating bat, using methods from evolutionary game theory.

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# Outline

- (1) Pursuit – brief history
- (2) Frames and models for pursuit
- (3) Dragonflies and aerial battles
- (4) Echolocating bats and prey capture
- (5) Sensorimotor feedback law
- (6) Why this law/strategy?

The talk is divided into 6 parts. After brief historical remarks and the presentation of basic models, we discuss pursuit in two biological contexts – dragonflies engaged in aerial battles and bats pursuing insect prey. The pursuit strategies in these two settings are geometrically indistinguishable and suggest sensorimotor feedback laws in two and three dimensions.

A basic question is why this strategy? We explore this question using evolutionary principles.

# 1. Pursuit – brief history



## Pursuit in the 19<sup>th</sup> century and before

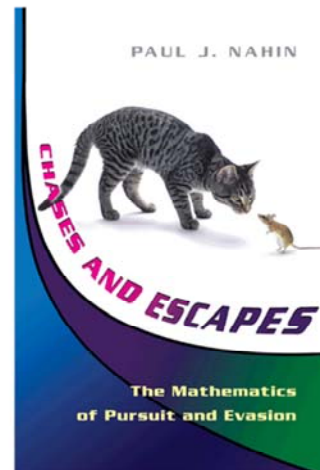
Pursuit has an interesting early history in recreational mathematics.

The problem of a pirate ship chasing a merchant ship.

Classical pursuit curve (\*\*\*)

The problem of 4 bugs (mice, dogs,...)

Cyclic pursuit (\*\*\*)



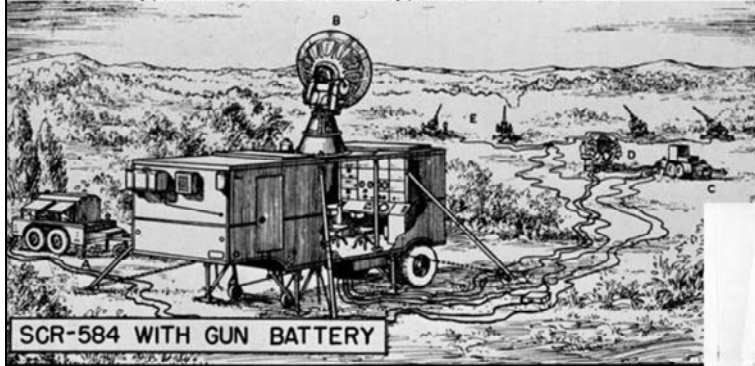
Classical pursuit stimulated a number of papers using calculus-based mathematics, many in the category of recreational mathematics. But it became serious business in WWII.

The problem of 4 bugs each pursuing the one to its left under strict classical pursuit is illustrated. For initial positions at the vertices of a square (or regular polygon) and all bugs moving at constant speed, there is a common meeting point.

Paul Nahin's excellent and entertaining book captures the mathematical spirit underlying classical pursuit, cyclic pursuit and other related modern developments.

## Pursuit in WW II

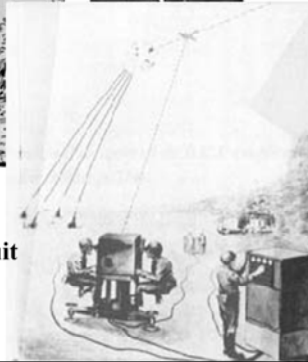
Work of **Hendrik W. Bode** and colleagues from Bell Telephone Laboratories on the M9-Director for coastal batteries in the south of England – the battle against V1 and V2



SCR-584 WITH GUN BATTERY

(A) Power generator (B) Radar set SCR-584 (C) Director M9  
(D) Follower for the M9 (E) 90mm battery

lead pursuit



P. Galison (1994), *Critical Inquiry*, 21(1):228-266.

D. Mindell (2002), *Between Human and Machine*, The JHU Press.

It is important to recall the role of Bell Labs engineers and mathematicians (led by Hendrik Bode) in creating an effective (deterministic) solution to the gun director problem. Two things contributed to the success of the Bell Labs solution based on **lead pursuit**: (a) The coupling of SCR-584 to the T10/M9 director; (b) Over a significant part of their flight, V1 and V2 traced straight line trajectories at steady altitudes. In comparison, Norbert Wiener's project based on statistical methods for the fire control problem did not succeed in leading to an implementation. One reason suggested was its complexity.

## Pursuit since the 1950's

The homicidal chauffeur problem of Rufus Isaacs - example from the theory of differential games.

Applications in missile guidance (N.A. Shneydor, 1998)

Recent – Bruckstein (ant algorithm) 1993 and later;  
Distributed consensus (Morse, Jadbabaie, Pappas, ...), 2000+  
Cyclic pursuit (Marshall, Broucke, Francis,...), 2003+  
and the biophysics literature;  
Idea of a set of systems meeting a common goal.

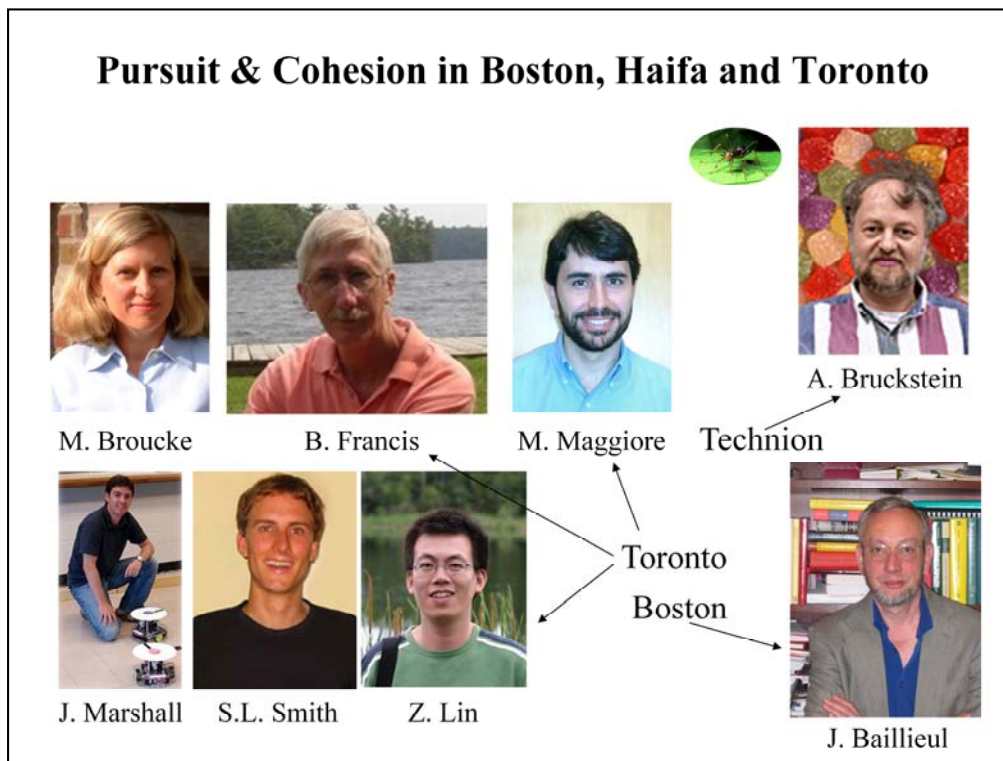
J. Baillieul and L. McCoy (2007), *Proc. 46<sup>th</sup> IEEE Conference on Decision and Control*.

A. Bruckstein (1993), *The Mathematical Intelligencer*, 15(2):59-62

J.A. Marshall, M.E. Broucke, and B.A. Francis (2006), *Automatica*, 42(1): 3-12.

The pioneering work of Isaacs in creating Differential Game Theory is one of the major highlights of the 1950's. This work was prompted by strategic and tactical missile defense considerations. See also the beautiful book of Shneydor on missile guidance. A number of groups have been active in linking pursuit questions to flocking and swarming. Besides the work of Bruckstein in the early 90's, on the ant algorithm, there have been developments in the consensus problem, and more recently on cyclic pursuit.

## Pursuit & Cohesion in Boston, Haifa and Toronto



Bruckstein demonstrated the idea that a trail of ants, engaged in classical pursuit, solves a problem of length minimization. There is more recent work on this problem by Dimitrios Hristu and his students, by Tom Richardson, and others.

The Toronto group demonstrated the idea that cyclic pursuit leads to cohesion in a group of robots.

John Baillieul and students have investigated pursuit for building formations in specific graph-theoretic contexts.

## 2. Frames and Models for Pursuit

We begin by setting up our basic mathematical models using the differential geometry of curves as a starting point.

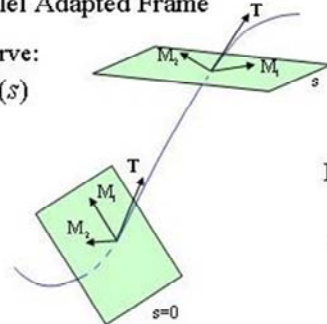
## Curves and natural frames

Natural Frenet or Relatively  
Parallel Adapted Frame

Regular curve:

$$s \mapsto \gamma(s)$$

$C^2$



Equations for relatively parallel adapted frame:

$$\gamma'(s) = T(s)$$

$$T'(s) = k_1(s)M_1(s) + k_2(s)M_2(s)$$

$$M_1'(s) = -k_1(s)T(s)$$

$$M_2'(s) = -k_2(s)T(s)$$

R. L. Bishop, *Amer. Math. Month.* (1975), **82**(3):246-251

$k_i$  are natural curvatures

Here we discuss how to set up models to describe pursuit problems. The basic idea is to think about parametrized curves and frames.

### Pursuit Model in 3D

The **natural curvatures** are controls. The speeds are time functions dictated by propulsive/lift mechanisms.

$$\dot{\mathbf{r}}_e = v_e \mathbf{x}_e$$

$$\dot{\mathbf{x}}_e = v_e (\mathbf{y}_e u_e + \mathbf{z}_e v_e)$$

$$\dot{\mathbf{y}}_e = -v_e \mathbf{x}_e u_e$$

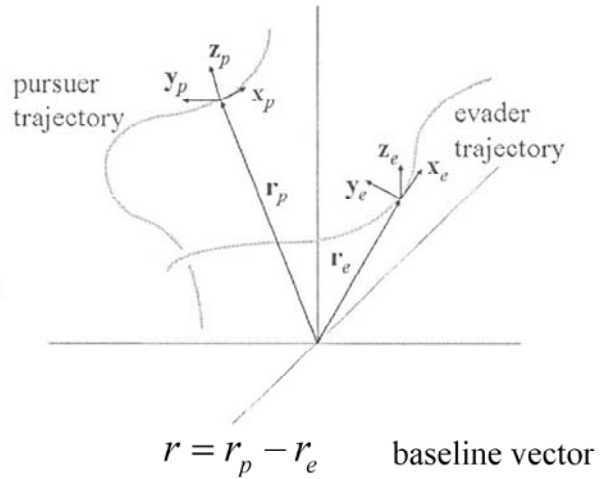
$$\dot{\mathbf{z}}_e = -v_e \mathbf{x}_e v_e$$

$$\dot{\mathbf{r}}_p = v_p \mathbf{x}_p$$

$$\dot{\mathbf{x}}_p = v_p (\mathbf{y}_p u_p + \mathbf{z}_p v_p)$$

$$\dot{\mathbf{y}}_p = -v_p \mathbf{x}_p u_p$$

$$\dot{\mathbf{z}}_p = -v_p \mathbf{x}_p v_p$$



The figure presents two curves with frames, one for the evader/target (denoted as e) and one for the pursuer (denoted as p). The curvatures  $u$  and  $v$  are controls. The speeds denoted by Greek letter nu are decided by propulsive/lift considerations.

## Three pursuit manifolds

<p>1. Classical pursuit (CP)</p>		$\frac{r}{ r } \cdot x_p = -1$
<p>2. Constant bearing pursuit (CB)</p>		$\frac{r}{ r } \cdot \text{Rot}(\theta)x_p = -1$
<p>3. Motion camouflage (MC)  <span style="color: red;">(dragonflies)</span>            Constant Absolute Target            Direction (CATD) <span style="color: red;">(bats)</span></p>		$\frac{r}{ r } \cdot \frac{\dot{r}}{ \dot{r} } = -1$

Classical pursuit is heading straight for target.

Constant bearing pursuit is heading with a fixed lead or lag.

Motion camouflage (with respect to infinity) is a stealthy pursuit nulling motion parallax, suggested by the trajectories of dragonflies.

As will be apparent further on, motion camouflage with respect to infinity is the same as a strategy adopted by bats in pursuit of insects. In that context, we use the more appropriate term CATD referring to constant absolute target direction.

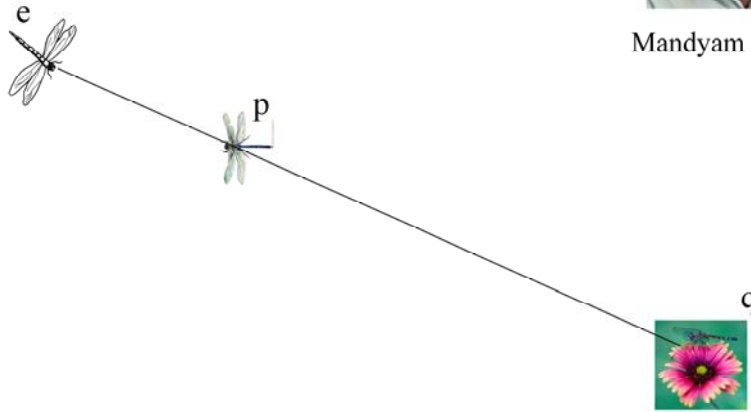


### 3. Dragonflies and Aerial Battles

## Motion Camouflage



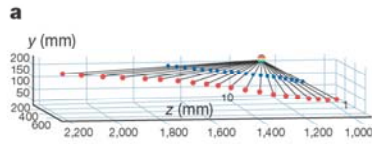
Mandyam Srinivasan



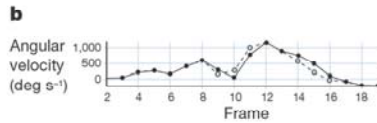
Srinivasan and Davey (1995), Proc. Roy. Soc. Lond. B 259(1354):19-25

The pursuer ( $p$ ) moves in such a way that the moving pursuee/target ( $e$ ) thinks ( $p$ ) is co-located with a familiar, stationary object ( $q$ ). Motion camouflage at infinity refers to the case where the object ( $q$ ) is at infinity. We idealize,  $p$ ,  $e$  and  $q$  as points. The ideas that insects execute such movement strategies was put forward by Srinivasan and Davey (hoverflies), Mizutani, Chahl and Srinivasan (dragonflies).

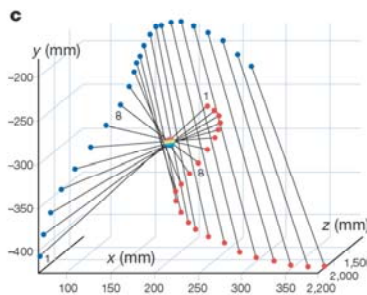
## Dragonflies - Aerial Battle Flight Data



a. Three dimensional reconstruction of territorial interaction of two male dragonflies *Hemianax papuensis*. Shadower – blue; Shadowee – red



b. Angular-velocity profile produced by the shadowing dragonfly in the shadowee's eye (filled circles) compared with that produced by a virtual stationary object at the intersection point (hollow circles).



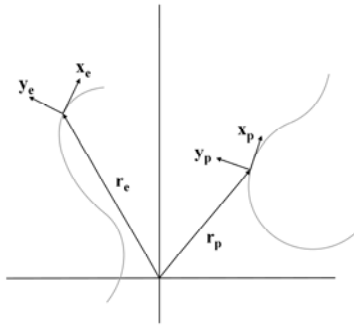
c. Another example – see frame 11+

From A. Mizutani, J.S.Chahl, and M.V. Srinivasan, "Motion camouflage in dragonflies," *Nature*, 423:604 p. 604, 2003.

<http://www.nature.com/nature/journal/v423/n6940/full/423604a.html>

This is from the Nature paper. There are three panels: top shows motion camouflage with respect to a finite point; middle shows visual angular velocity matches between a fixed feature and a moving pursuer; bottom shows an instance in which there is a switch from MC with respect to a finite point to a MC with respect to a point at infinity.

## Modeling Motion Camouflage (1)



$$\begin{aligned}\dot{r}_p &= x_p \\ \dot{x}_p &= y_p u_p \\ \dot{y}_p &= -x_p u_p\end{aligned}\quad (1)$$

$$\begin{aligned}\dot{r}_e &= v x_e \\ \dot{x}_e &= v y_e u_e \\ \dot{y}_e &= -v x_e u_e\end{aligned}\quad (2)$$

Here we specialize the models of section 2 to the plane. The speed ratio is given by  $v$ , assumed constant and less than 1 in what follows.

The MC model – pursuit model; speed ratio is given by  $\nu$ .

## Modeling Motion Camouflage (2)

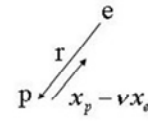
Motion camouflage with respect to a point at infinity is given by

$$r \triangleq r_p - r_e = \lambda r_\infty \quad (3)$$

Where  $r_\infty$  is a fixed unit vector and  $\lambda$  is a time-dependent scalar. Infinitesimally, motion camouflage with respect to  $\infty$  is equivalent to

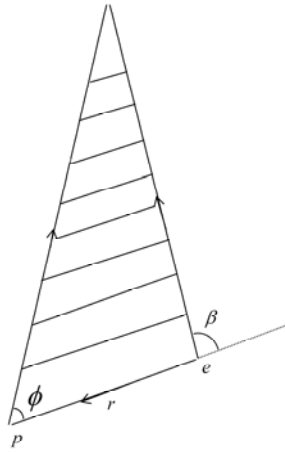
$$\begin{aligned} w &\equiv \dot{r} - \left( \frac{r \cdot \dot{r}}{|r|} \right) \frac{r}{|r|} \\ &\equiv 0 \end{aligned} \quad (4)$$

(here we restrict to non-collision states, i.e.  $|r| \neq 0$  )



$w$  denotes the transverse relative velocity.

## Rectilinear Case of Motion Camouflage



$$u_e \equiv 0$$

$$\text{If } \phi = \sin^{-1}(v \sin \beta)$$

$$\text{then } u_p \equiv 0$$

maintains motion camouflage

Pursuee travels in a straight line. There is a straight line trajectory for the pursuer which is the time-optimal intercept trajectory.

## Control Problem

Determine a **feedback law** for steering the pursuer such that, under suitable hypotheses on evader behavior, the system “enters” the manifold of motion camouflage states

$$S^1 \times \mathbb{R}^1 \times SE(2) \cup S^1 \times \mathbb{R}^1 \times SE(2) .$$

Need a way to measure distance to this manifold

The two components here correspond to two different signatures (see next slide). Only one is a pursuit manifold, i.e. range shortening.

## A Distance Function

$$\begin{aligned} \text{Let } \Gamma &\triangleq \left( \frac{d}{dt} |r| \right) / \left| \frac{dr}{dt} \right| \\ &= \frac{r \cdot \dot{r}}{|r| |\dot{r}|} \end{aligned} \quad (6)$$

well-defined on non-collision states.

Observe  $-1 \leq \Gamma \leq 1$  ,  $1 - \nu \leq |\dot{r}| \leq 1 + \nu$

$$\text{and } 1 - \Gamma^2 = \frac{|w|^2}{|\dot{r}|^2}$$

Driving  $\Gamma$  to  $\pm 1$  corresponds to reducing distance to motion camouflage manifold

As	$\Gamma \rightarrow +1$	baseline lengthening
As	$\Gamma \rightarrow -1$	baseline shortening



## Finding a Feedback Law

Compute  $\dot{\Gamma}$  (as a function of  $u_p, u_e$  etc.)

Find law for  $u_p$  to make  $\dot{\Gamma}$  negative (in a suitable region).

Consider

$$u_p = -\mu \left( \frac{r}{|r|} \cdot \dot{r}^\perp \right) + \left[ \frac{(x_p \cdot x_e) - v}{1 - v(x_p \cdot x_e)} \right] v^2 u_e \quad (7)$$

For any  $\mu > 0$  there exists  $r_0 > 0$  such that under (7),

$$\dot{\Gamma} \leq 0, \quad \forall |r| > r_0$$

But, second term in (7) asks for too much information.

## Finding a Feedback Law

Consider keeping first term only in (7), but add hypothesis that  $|u_e|$  is bounded.  
Thus

$$u_p = -\mu \left( \frac{r}{|r|} \dot{r}^\perp \right) \quad (8)$$

### Definition

For the pursuit-evader system (1), (2) with  $\Gamma$  defined by (6), we say that motion camouflage is accessible in finite time if for any  $\varepsilon > 0$ , there exists a time  $t_1 > 0$  such that

$$\Gamma(t_1) \leq -1 + \varepsilon$$

E.W. Justh and P. S. Krishnaprasad (2006), *Proc. R. Soc. A*, 462:3629-3643.

P.V. Reddy, E.W. Justh and P. S. Krishnaprasad (2006), *45<sup>th</sup> IEEE CDC*, pp.3327-3332.

## High Gain Feedback

**Proposition:** For system (1)(2),  $\Gamma$  as in (6) and control law (8), with the following hypotheses:

(A1)  $0 < \nu < 1$  (and  $\nu$  is constant)

(A2)  $u_e$  is continuous and  $|u_e|$  is bounded

(A3)  $|r(0)| > 0$  and

(A4)  $\Gamma_0 = \Gamma(0) < 1$

Then motion camouflage is accessible in finite time using high-gain feedback (i.e., choosing  $\mu > 0$  sufficiently large).

## Connections to Missile Guidance

A well-known law in missile guidance is

$$\mathbf{u}^{PPNG} = N\dot{\lambda}, \quad (9)$$

where  $\dot{\lambda}$  = rotation rate of baseline. Our law (8) take the form

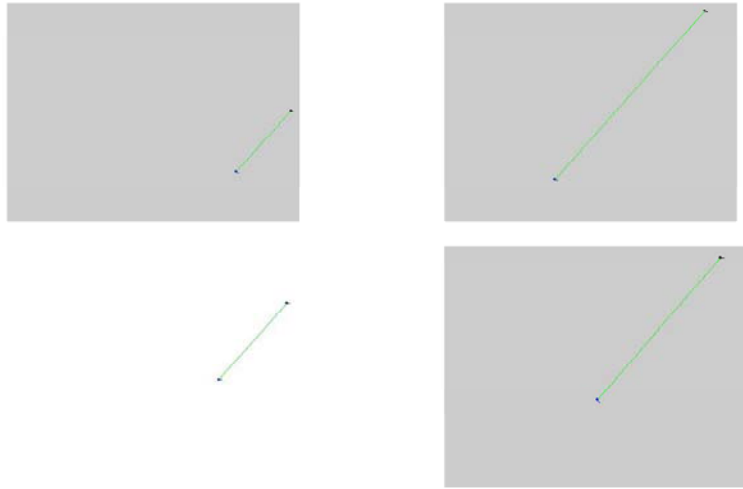
$$\mathbf{u}^{MCPG} = N \frac{|r|}{r_0} \dot{\lambda}.$$

Range information is needed. Bats use range information effectively.

Optic flow computes  $\dot{\lambda}$

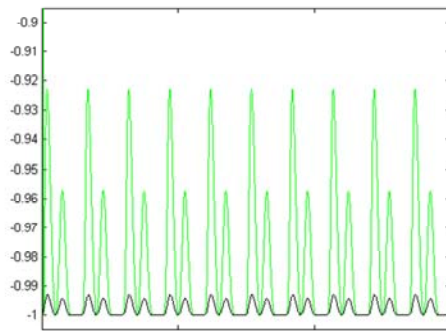
Recall a well-known guidance law in missile guidance theory and practice: the proportional navigation law. Motion camouflage proportional guidance corresponds to adjusting the navigation constant in a range-dependent way. The angular rate is determined from optic flow in visual insects.

## Simulations of Motion Camouflage Law

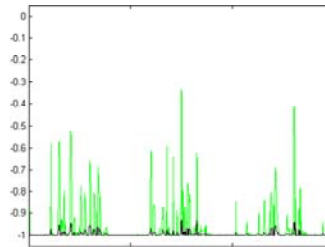


In these 4 panels the upper left corresponds to the rectilinear case; the upper right corresponds to the case of pursuee in a circular motion; in the lower left, the pursuee engages in a sinusoidal motion; in the lower right the pursuee is doing random turns

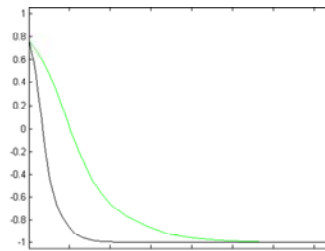
## Diagnostics on Distance Function



Sinusoidal case



Random evader case



Initial fast transient for random evader case

The green curves correspond to lower gain values; the blue curves correspond to higher gain values. In the panel on lower right the time scale is stretched to see the initial transient of Gamma decreasing down to nearly -1.

## 4. Echolocating Bats and Prey Capture

Here we begin our story of echolocating bats and their behavior in pursuing prey insects. We discuss the use of models introduced earlier, in understanding data gathered in the Auditory Neuroethology Laboratory.

## Bats and Pursuit

Sensory (What the bat knows?)

Motor (What the bat does?)

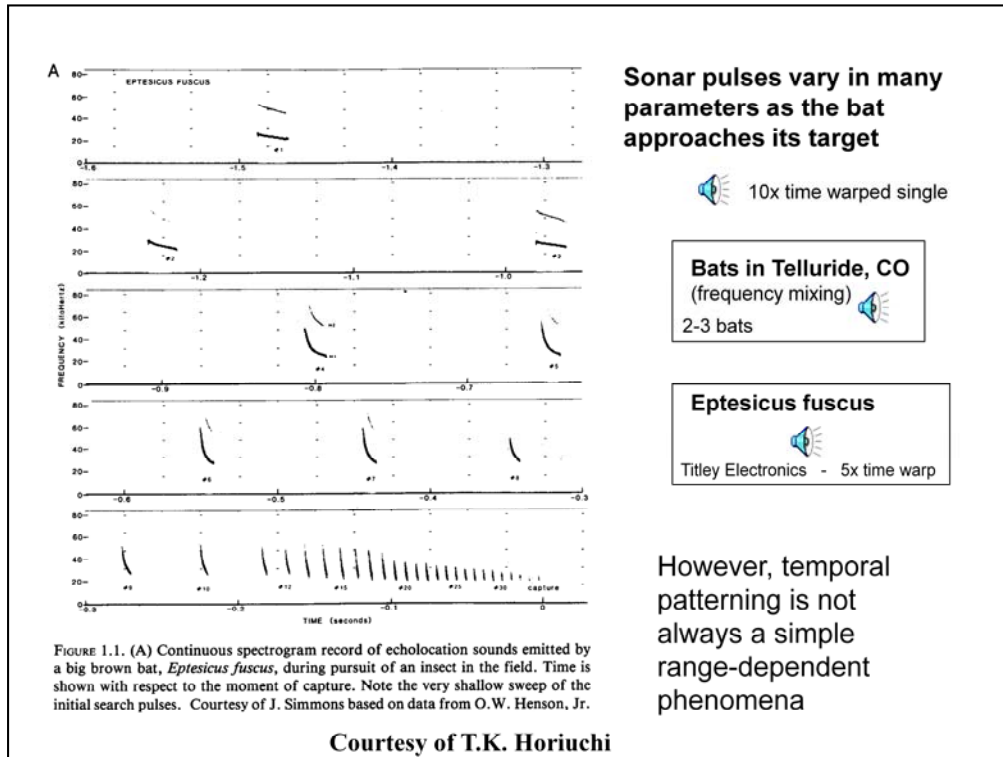
Sensorimotor (What is the law?)

We begin with some historical remarks on the early work that has helped reveal what the bat knows about the world around it. In the lab, experiments on bat behavior have raised questions about what sensorimotor feedback laws are being used.

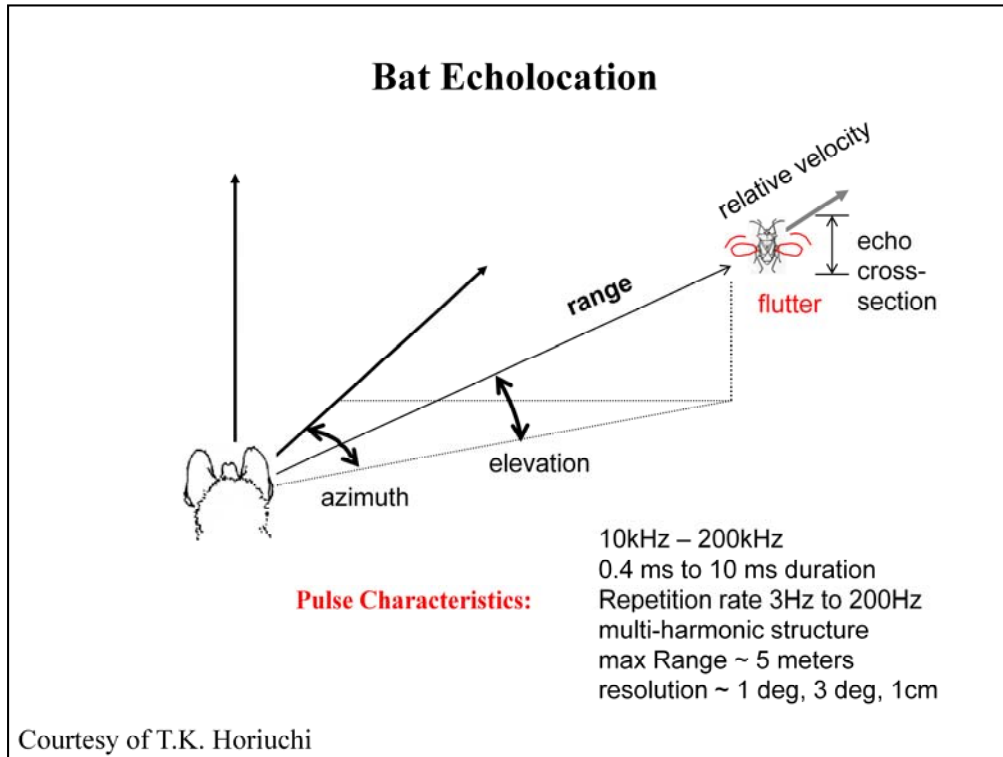




Spallanzani was a prominent Physiologist. He investigated the problem of the “sixth sense” in bats. He systematically moved towards the conclusion that vocalization AND hearing were important to the bat’s ability to navigate successfully in the dark in complex environments. The experimental work and insights of contemporary Swiss scientist Louis Jurine of Geneva were important in reaching this conclusion. But the critical idea that ultrasound was the probing signal was not known to these pioneers, since the very existence of such sounds was not known. One had to wait till the 1930’s and the work of Donald Griffin, George W. Pierce and Robert Galambos. In their experiments (1938-1941), a special microphone in a dark room was used to prove that bats flying in the dark could “see” by emitting ultrasonic vocal sounds and then navigating around obstacles using the echoes as an internal guidance system. Such flight was severely impaired if either a bat’s ears were plugged, or its mouth was held closed by a loop of thread.



The big brown bat generates an ultrasonic chirp whose many parameters are manipulated in an appropriate manner for prey capture. The bat is known to modulate the: amplitude, duration, sweep-trajectory, bandwidth, and repetition-rate. While bats of other species are known for their ability to utilize Doppler effects, the big brown bat is not known to utilize this feature of the signal. In this figure, the spectrogram is shown for an approach and capture sequence in the big brown bat. While this record only shows the first two harmonics due to measurement limitations, a third harmonic is known to be a strong feature of this species.



echolocation is used to:

- (1) detect objects,
  - (2) behaviorally classify objects
  - (3) extract range
  - (4) extract azimuth,
  - (5) extract elevation,
  - (6) determine relative velocity
- mostly ultrasonic
  - duration = 0.1 ms to 10 ms
  - repetition rate = 10 Hz to 100 Hz
  - multi-harmonic downward frequency sweep
  - range = < 5 meters
  - range resolution = ~ 1cm
  - azimuthal resolution = 1 deg
  - elevation resolution ~ 3 deg

## Prey Capture Experiments



Copyright Bat Photography LLC (J.S. Altenbach)



*Eptesicus fuscus*

vs.

*Parasphendale agrionina*

Praying mantids have hearing organs in the abdomen, sensitive in the ultrasonic range. Thus they are equipped with a countermeasure to escape bats that hunt them. In the experiments reported in the following, the hearing organ of *Parasphendale agrionina* is partially disabled by application of Vaseline.

**Batlab Flight Data (1)**

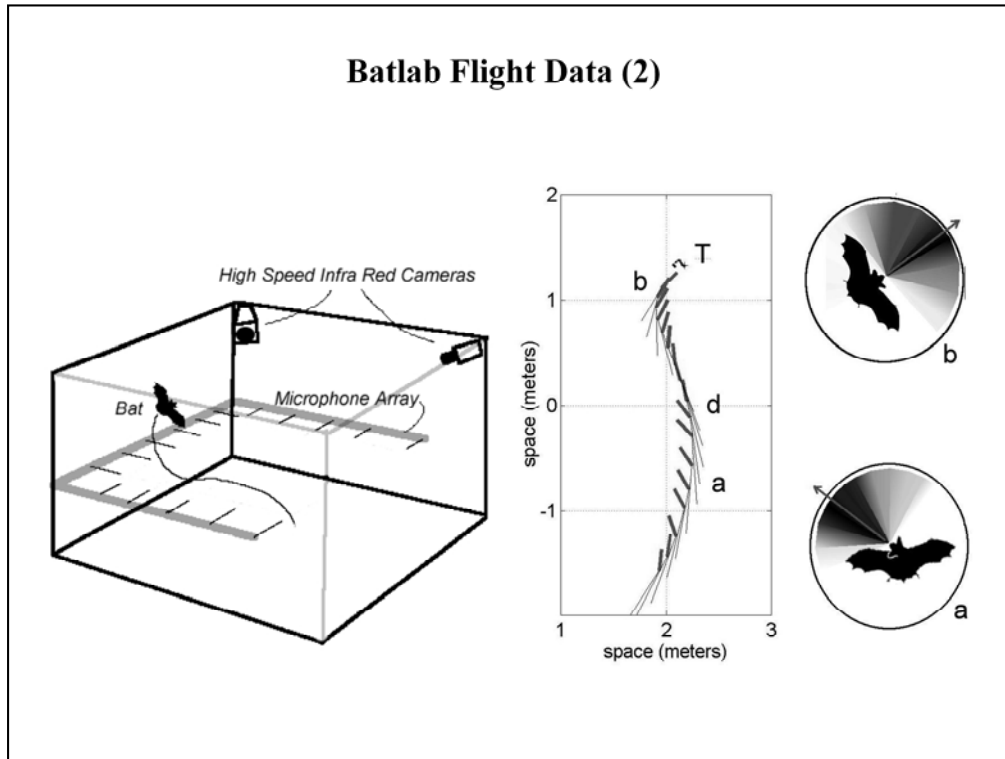
Echolocating FM bat, *Eptesicus fuscus*



Courtesy of Cynthia Moss and Kaushik Ghose, NACS, University of Maryland  
<http://www.bsos.umd.edu/psyc/batlab/index.html>

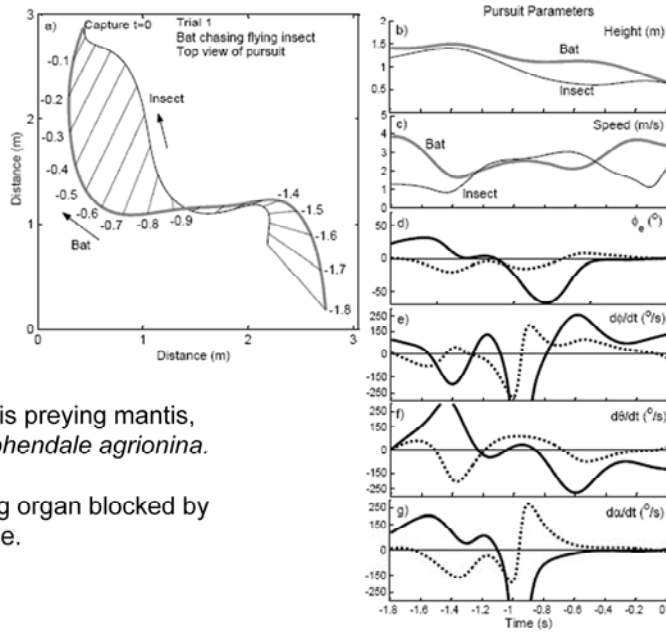
Video of bat-insect encounter.

## Batlab Flight Data (2)



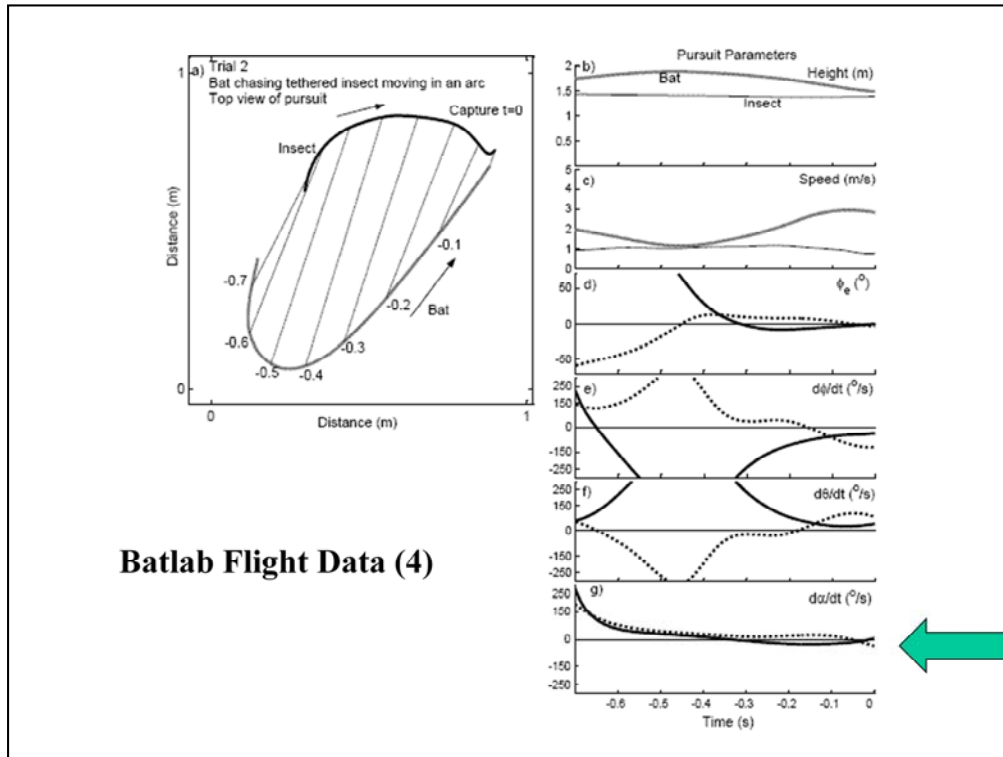
This picture shows the layout of the flight room and the representation of bat head direction. For a fixed target T the bat eventually aligns head direction and flight direction with target direction.

### Batlab Flight Data (3)



Target is preying mantis,  
*Parasphendale agrionina*.  
Hearing organ blocked by vaseline.

Focus on the bottom of the set of plots to the right (see green arrow). This is a plot of the angular rate of the bat-insect baseline, expressed in terms of azimuth and elevation angles. Note that this rate decays to zero, indicating convergence to a state of constant absolute target direction.



In this bat is chasing an artificially moved target. It makes a wide U turn before capture. Again CATD applies (see green arrow).



## Summarizing the Data

From mariners avoiding collision courses, to baseball outfielders catching flyballs, the **constant bearing (CB)** strategy has been known as an effective strategy.

Here we see bats executing a different strategy – keeping **constant absolute target direction (CATD)**, geometrically indistinguishable from what we referred to earlier as **motion camouflage with respect to infinity**.

K. Ghose and C.F. Moss (2006), *J. Neuroscience*, 26(6):1704-1710.

K. Ghose, T.K. Horiuchi, P.S. Krishnaprasad and C.F. Moss (2006), *PLoS Biology*, 4(5), 865-873, e108.

## 5. Sensorimotor Feedback Law

Here we consider a generalization to 3D of the motion camouflage pursuit law derived earlier. A detailed computational investigation of bat-insect trajectories is used to examine the support for such laws in the data. Delay matters. There was a poster presentation (We122.9) on Wednesday afternoon (P.V. Reddy, E.W. Justh and P. S. Krishnaprasad – “Motion camouflage with sensorimotor delay”) of the underlying theory.

### Feedback Law for 3D

$$\dot{\mathbf{r}}_p = v_p \mathbf{x}_p$$

$$\dot{\mathbf{x}}_p = v_p (\mathbf{y}_p u_p + \mathbf{z}_p v_p)$$

$$\dot{\mathbf{y}}_p = -v_p \mathbf{x}_p u_p$$

$$\dot{\mathbf{z}}_p = -v_p \mathbf{x}_p v_p$$

$$\dot{\mathbf{r}}_e = v_e \mathbf{x}_e$$

$$\dot{\mathbf{x}}_e = v_e (\mathbf{y}_e u_e + \mathbf{z}_e v_e)$$

$$\dot{\mathbf{y}}_e = -v_e \mathbf{x}_e u_e$$

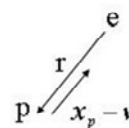
$$\dot{\mathbf{z}}_e = -v_e \mathbf{x}_e v_e$$

$$\mathbf{r} = \mathbf{r}_p - \mathbf{r}_e$$

$$u_p = -\mu \left[ \left( \dot{\mathbf{r}} \times \frac{\mathbf{r}}{|\mathbf{r}|} \right) \cdot \mathbf{z}_p \right]$$

$$v_p = \mu \left[ \left( \dot{\mathbf{r}} \times \frac{\mathbf{r}}{|\mathbf{r}|} \right) \cdot \mathbf{y}_p \right]$$

This law drives the system to the manifold



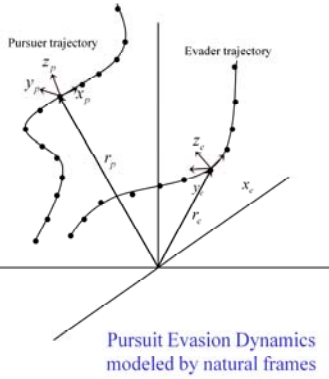
Reddy, P.V., E.W. Justh, and P.S. Krishnaprasad (2006). *Proc. 45th IEEE Conf. Decision and Control*, pp. 3327-3332.

Inspired by our results in the planar motion camouflage problem, we write down a biologically plausible feedback law. The law depends on quantities such as bat-insect range and relative angular velocity. Under suitable hypotheses, Reddy et. al. show that the law above drives the closed loop system to the manifold of motion camouflage (CATD) in finite time.

Do bats use such a law in prey capture?

## Extracting Curvatures by Regularized Inversion (RI)

Given sampled bat and insect trajectories, extract smoothed curvatures, speed signals and associated frame information (including the optimal initial frame).



$$\min \left( \sum_{k=0}^N \left( |\gamma(k) - \gamma(kT)|^2 + \lambda \int_{kT}^{(k+1)T} (\dot{u}^2 + \dot{v}^2 + \dot{U}^2) dt \right) \right)$$

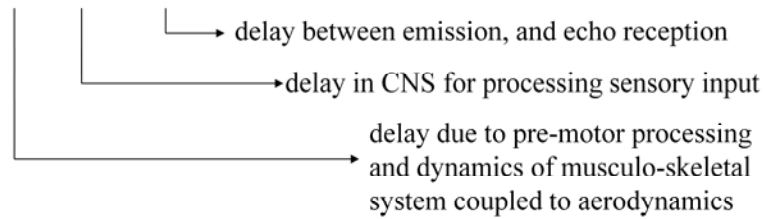
- $\lambda$  -- regularization parameter, controls amount of smoothing.
- For noisy data a large  $\lambda$  should be used (c.f. cross validation approach of Grace Wahba and collaborators)
- Algorithm is capable of estimating curvatures with high resolution, i.e., sub frame adaptable.

$$\begin{aligned} \dot{r}_p &= v_p x_p & \dot{r}_e &= v_e x_e \\ \dot{x}_p &= v_p (u_p y_p + v_p z_p) & \dot{x}_e &= v_e (u_e y_e + v_e z_e) \\ \dot{y}_p &= -v_p u_p x_p & \dot{y}_e &= -v_e u_e x_e \\ \dot{z}_p &= -v_p v_p x_p & \dot{z}_e &= -v_e v_e x_e \end{aligned}$$

We formulate a problem of determining controls (curvatures, speeds) for generative models based on moving frames, from sampled data (of locations of bat and insect). Our approach is to solve a regularized optimization problem. The optimization process yields, frames and controls.

## The Need to Include Delay

$$\text{Time delay} = \delta_{motor} + \delta_{auditory} + \delta_{echo}$$



**MODIFIED HYPOTHESIS:** The sensorimotor loop of the bat uses a delayed version of the feedback law presented in the previous slides.

$$\hat{u}_p(t-\delta) = - \left[ \left( \dot{r} \times \frac{r}{|r|} \right) \cdot z_p \right]_{(t-\delta)}$$

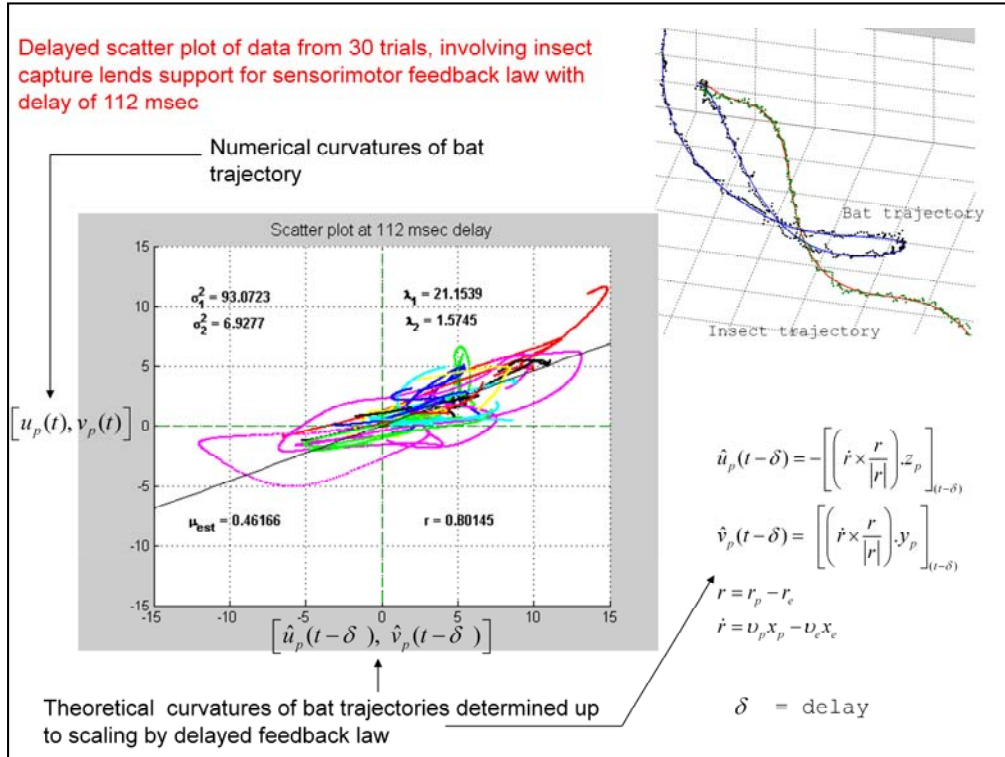
$$\hat{y}_p(t-\delta) = \left[ \left( \dot{r} \times \frac{r}{|r|} \right) \cdot y_p \right]_{(t-\delta)}$$

$$r = r_p - r_e$$

$$\dot{r} = v_p x_p - v_e x_e$$

Reddy, P.V., E.W. Justh, and P.S. Krishnaprasad (2007), 46<sup>th</sup> IEEE CDC, WeP122.9

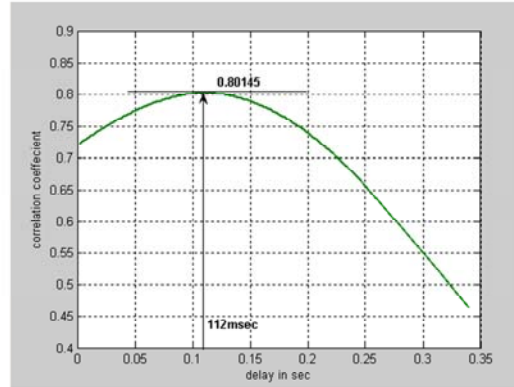
See analysis of delayed feedback laws in pursuit from Wednesday Poster presentation.



This figure summarizes the outcome of a statistical examination of the hypothesis that in insect pursuit, a bat uses a delayed feedback law that is linear in the rate of rotation of the baseline from the bat to the insect. Video data from two infra-red cameras in the flight room was used to obtain trajectory data for insect and bat at a sampling rate of once every 4 msec. Using an optimization method for regularization of ill-conditioned problems, we obtained numerically the instant-by-instant trajectory curvatures of the bat, from the sampled trajectories. These numerical curvatures are then plotted against a delayed version of the hypothetical feedback law, where the delay accounts for the overall latency in the response of the bat to changes in the flight of the insect, including sensorimotor neural computation, biomechanical delay and aerodynamics. A range of delays was considered, and the best delay (in the sense of maximum correlation, here 0.80145), turned out to be about 112 msec. This best delay is consistent with other known estimates in the literature. The results show the effectiveness of the pursuit strategy employed by the bat, based on directional and target range cues obtained by biosonar even in the presence of delay. The technological implications of similar sensori-motor strategies in robotic assist systems for humans are being explored through experiments in the Computational Sensorimotor Systems Laboratory, and the Intelligent Servosystems Laboratory, of the University of Maryland.

## Statistical Evaluation

$$\rho_{[u_p(t), v_p(t)][\hat{u}_p(t-\delta), \hat{v}_p(t-\delta)]}$$



P.V. Reddy, K. Ghose, E.W. Justh, T.K. Horiuchi, P.S. Krishnaprasad, and C.F. Moss, in preparation, 2007

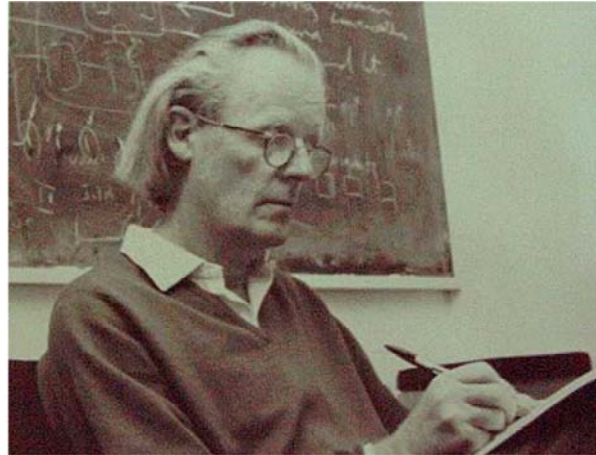
Delay vs. correlation

## 6. Why this Law?

In the context of engineering design, we choose a control law that meets performance objectives subject to constraints. When we encounter a control law in nature persistently, it is not clear there is an overarching performance measure being optimized. Instead, one seeks an evolutionary basis for the phenomenon. In the previous section of the talk we see the prevalence of a control law – CATD, in bat-insect prey-capture behaviors. We give a preliminary answer to the question of prevalence of CATD via the theory of evolutionary games.



## John Maynard Smith (engineer-biologist)



J. Maynard Smith and G.R.Price (1973). *Nature*, **246**:15-18.  
J. Maynard Smith (1982). *Evolution and the Theory of Games*, Cambridge U. Press.  
P. D. Taylor and L. Jonker (1978). *Math. Biosciences*, **40**:145-156.  
J. Hofbauer and K. Sigmund (2003), *Bull. AMS* (new series), **40**:479-519

R.A. Fisher, William Donald Hamilton, John Maynard Smith all addressed fundamental questions in biology – what is the genetic basis for 1:1 sex ratio? why certain behavioral strategies prevail?, etc.

John Maynard Smith (who trained as an aeronautical engineer at Trinity College, Cambridge, and designed aeroplanes during WW II before starting afresh in biology), and George Price, formulated Evolutionary Game Theory in their famous 1973 paper. A key concept of the theory was that of an evolutionarily stable strategy (ESS). It was anticipated in John Nash's thesis (Non-cooperative Games, 1950, Mathematics Department, Princeton University) in two paragraphs that did not find their way into Nash's journal publications.

In 1978, Taylor and Jonker gave a differential equation model for the Maynard Smith – Price formulation. These equations and variants have had, and continue to have, tremendous impact on evolutionary perspectives in biology, economics, and more recently linguistics.

## Evolutionary Dynamics

Maynard Smith and Price suggested a deterministic mutation-selection dynamics in which, given a population with frequencies

$p_1, p_2, \dots, p_n$

of strategies (phenotypes), encounters between individuals of the population associated to different strategies lead to mutations that alter the frequencies in the next generation according to fitness :

$$p_i \rightarrow p_i(F_i(p)/\bar{F}(p)) ,$$

where the frequency-dependent fitness





$$F_i = F_i(p)$$

and

$$\bar{F} = \sum_1^n p_i F_i$$

is the average fitness.

Hawk-Dove Model: Costs and Benefits of Fighting over Resources

Payoff to...	...in fights against:	
	hawk	dove
hawk	 Hawk wins 50% of fights; is injured in 50% of fights. Payoff: $(V-D)/2$	 Hawk always wins; dove flees. Payoff: $V$
dove	 Dove never wins; is never injured. Payoff: $0$	 Dove wins 50% of fights; is never injured; wastes time. Payoff: $V/2-T$

$V$  = fitness value of winning resources in fight  
 $D$  = fitness costs of injury  
 $T$  = fitness costs of wasting time  
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For Maynard Smith and Price, the hawk-dove game and its variants served as key examples. In this case the fitness functions are linear with matrix given as in the figure on lower right. The evolutionary dynamics in this example determined how a population with a mixture of “hawk” and “dove” strategies evolves through repeated encounters. Thus the dynamics models a selection process. A differential equation form of the above dynamics is given by the replicator dynamics in the next slide.

**Note 01/02/2009** – here I refer to strategies as (behavioral) **phenotypes**. This is consistent with how Maynard Smith discusses game theory in the study of animal conflicts within a species. The replicator equations are for the dynamics of **phenotype frequencies**. Dawkins (The Extended Phenotype, 1982) gave a justification for viewing strategies as replicators. But authors such as Benaim, Schreiber, Pemantle end up referring to **strategies as genotypes**. This is perhaps a confusion with the usage in population genetics where indeed frequencies are associated to alleles (genotype) and once again we write down replicator equations for frequencies, here for **genotypes**. The story is clear when reading (K. Sigmund (1986), “A survey of replicator equations,” ch. 4 of, J.L. Casti and A. Karlqvist (eds.) Complexity, Language, and Life: Mathematical Approaches, Springer-Verlag, Berlin, 1986.)

## Replicator Dynamics

$$\dot{p}_i = p_i[F_i(p) - \bar{F}] \quad \text{for } i = 1, 2, \dots, n,$$

Here  $p = (p_1, p_2, \dots, p_n) \in S^n$  the probability simplex

$F_i(p)$  = fitness of  $i^{\text{th}}$  strategy

and  $\bar{F} = \sum_1^n p_i F_i(p)$  is the average fitness

linear fitness functions :  $F_i = \sum_{j=1}^n a_{ij} p_j$

See D. Foster and H.P. Young (1990), *Theor. Pop. Biol.* 38:219-232, for a stochastic version.

Replicator dynamics is best viewed as a closed loop system associated to the feedback (selection) process that changes the frequencies of strategies within a population according to the payoffs. Replicator dynamics above constitute one approach to capturing the selection process: more successful strategies spread in the population.

The relationship between Nash equilibria for the game defined by the matrix A (for the case of linear fitness functions) and the equilibria of the replicator dynamics is known as the folk theorem of evolutionary game theory: (i) If  $z$  is a strict Nash equilibrium it is an asymptotically stable equilibrium of the replicator dynamics; (ii) if the rest point  $z$  is the limit of an interior orbit for  $t \rightarrow \infty$ , then  $z$  is a Nash equilibrium; (iii) if the rest point is stable, then it is a Nash equilibrium.

Many variants of the replicator dynamics exist, some now understood as going back to the 1950's in von Neumann's search to find differential equations that compute min-max solutions to zero-sum games. More recently, by adding white noise to the replicator dynamics, Foster and Young launched a program of stochastic modeling of evolutionary selection.

## An Evolutionary Game (experiment)

Three (3) sets, each consisting of  $N$  simulated **bat-insect encounters**, with termination if spatial separation becomes smaller than a specified threshold, or the clock runs out.

In each trial/encounter, initial conditions and insect steering behavior are randomized.

In each set, bat uses one of three control laws (respectively associated to CP, CB, or CATD).

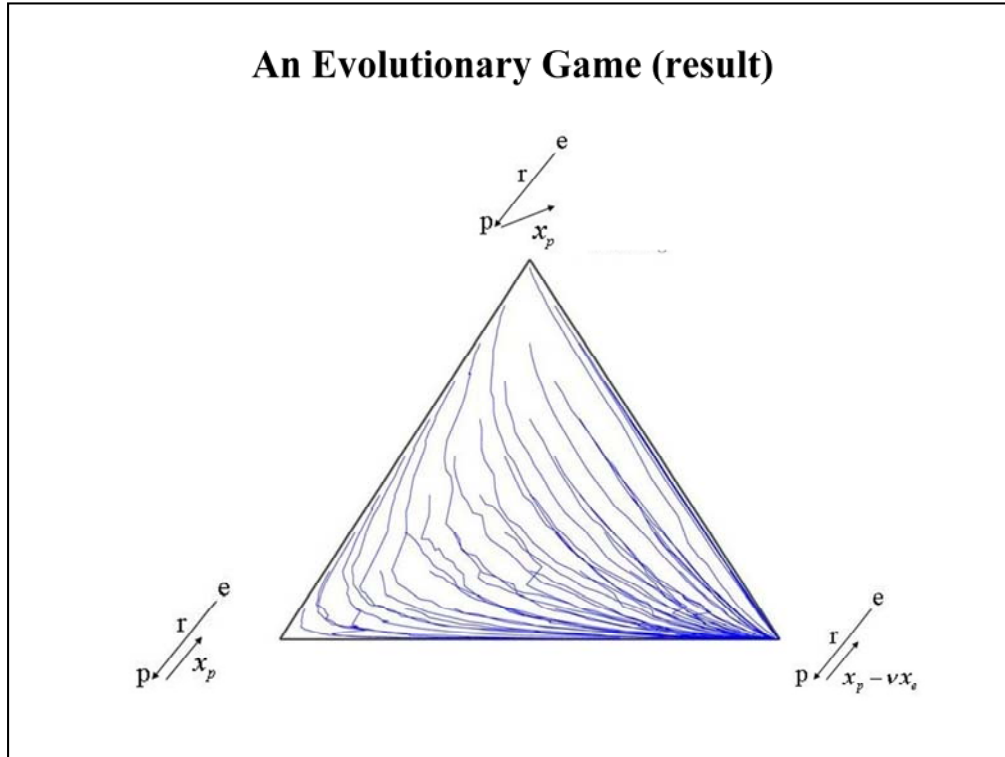
$$F_i = \frac{1}{N} \sum_{k=1}^N \frac{1}{\tau_k^i}, \text{ for } i=1,2,3 \text{ (indicating control laws)}$$

and,  $\tau_k^i$  denotes encounter duration

Ermin Wei (2007), Senior thesis

We carried out a set of simulation experiments to understand the evolutionary dynamics of bat pursuit behavior. Each play of the game consisted of a simulated bat pursuing a simulated insect (in 2D) using a specific pursuit law, until it gets close enough or time runs out. The initial conditions for the bat and the insect and the steering behavior of the insect were randomized. The fitness measure of a control law, computed from a set of plays using that law, is based on the principle that longer the encounter lower is the payoff. Sample averages are used for fitness.

## An Evolutionary Game (result)



The stochastically computed trajectories of replicator dynamics in the simplex appear to be all attracted to the equilibrium pure strategy we call motion camouflage or CATD. We continue to work along these lines to gain insight into the evolutionary game formalism as a means to understand biological sensorimotor behavior.

## Final Remarks

- We have seen that it is possible to investigate and derive sensorimotor feedback laws in two biological settings, using a **geometric perspective**. As a system that relies on active perception, the echolocating bat is of special interest.
- These laws, in the broad category of pursuit laws, very likely have been arrived at in nature through **evolutionary** processes.
- There is a **game-theoretic** approach to investigating evolutionary processes that merits attention in control theory.
- Insights from **pursuit** laws need to be integrated in seeking laws for **cohesion**, including how cooperative behavior evolved.